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New Evidence Against Tupaioid Affinities of the Mammalian Family Anagalidae¹

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A previously unknown extinct family, the Anagalidae, was added to the prosimian primate superfamily Tupaioidea by G. G. Simpson in 1931. The Anagalidae were originally based on a single specimen of *Anagale gobiensis* from the Tertiary of Inner Mongolia. Since 1931 *Anagale* has become embedded in the voluminous secondary literature on fossil primates, and the genus has been generally accepted as the only known fossil tupaioid primate. No additional remains of *Anagale* have ever been reported, nor was any close relative of *Anagale* known until 1951, when Bohlin described *Anagalopsis kansuensis* from the Tertiary of Kansu.

Among the treasures collected by the 1928 Central Asiatic Expedition were two specimens of *Anagale gobiensis*, not just one. Both were collected from sediments correlated with the Ulan Gochu Formation (early Oligocene), and both were obtained in an area of badlands ("East Mesa") east of the Shara Murun Valley of Inner Mongolia (approximately longitude 111° 30' E., latitude 42° 30' N.). One of the two specimens is the beautifully preserved skull, jaws, and fragmentary skeleton from "Twin Oboes" which was made the type specimen of *Anagale gobiensis* by Simpson in 1931. The other specimen, a fragmentary skull and

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jaws from Jhama Obo, remained completely incased in a concretion until 1962, when it was discovered by James S. Mellett and the concretionary matter removed by the use of an Airbrasive machine. Although the teeth of the new specimen are not so well preserved as those of the type, they are less worn than either the latter or the teeth of *Anagalopsis kansuensis*. The new specimen sheds valuable light on the dental morphology of *Anagale*, and previously unknown details of the anagalid tooth crown pattern can now be studied. Because *Anagale* was referred to the tupaoid lemuriform primates by Simpson and others, but completely removed from the Lemuriformes and placed in the Mammalia, *incertae sedis*, by Bohlin, the newly discovered material is described here in order to throw new light on the problem of anagalid affinities. The new evidence favors Bohlin's argument.

CLASS MAMMALIA

INFRAClass EUTHERIA, *INCERTAE SEDIS*

FAMILY ANAGALIDAE SIMPSON, 1931

GENERA: *Anagalopsis* Bohlin, 1951, ?Oligocene, Kansu; and *Anagale* Simpson, 1931, early Oligocene, Inner Mongolia.

REMARKS: The family Anagalidae contains only two described genera, *Anagale* and *Anagalopsis*. *Anagale* has received much attention in the secondary literature, but the only first-hand research to reach print is Simpson's. *Anagalopsis* has received much less attention, and the only first-hand discussion of its morphology is that of its original discoverer, who removed it from the primates. *Anagale* and *Anagalopsis* are so similar, however, that they must be placed in the same family of mammals, even though Bohlin (p. 46) believed that they should be placed in separate families because of certain supposed significant differences. The main supposed difference between them, the construction of the bullae in the two genera, is shown below to be non-existent, and the remaining differences do not merit more than generic rank.

Anagale gobiensis Simpson, 1931

Figures 1-6

TYPE: A.M.N.H. No. 26079, nearly perfect skull and jaws, with much of skeleton; collected at "Twin Oboes," "East Mesa," east of Shara Murun Valley, Inner Mongolia.

REFERRED SPECIMEN: A.M.N.H. No. 26141, fragmentary rostrum lacking the premaxillae, but with jaws in occlusion with the upper

TABLE 1
MEASUREMENTS (IN MILLIMETERS)

| | <i>Anagale gobiensis</i> | | <i>Anagalopsis kansuensis</i> |
|--|-----------------------------|-----------------------|-------------------------------|
| | A.M.N.H. No. 26079, Type | A.M.N.H. No. 26141 | A.M.N.H. No. 56003, Cast |
| Length/width, P ¹ | 2.7/1.6 | 2.3/1.2 | — |
| Maximum anteroposterior diameter, P ² | 2.9+ | 3.2 | 3.4 |
| Maximum length, P ¹ –M ³ | 22.3–22.7 | 21–22 ^a | 27.5 ^a |
| Maximum length, P ² –M ³ | 18.9 | 18–19 ^a | 23.9 |
| Maximum length, P ₄ | 3.3 | 3.3 | 3.7+ |
| Width of trigonid base, P ₄ | 2.4–2.5 | 2.4 | 3.8 |
| Width of talonid base, P ₄ | 2.2 ^a | 2.3 | 3.3 |
| Maximum length, M ₁ | 3.7 | 3.6 | 4.2+ |
| Width of trigonid base, M ₁ | 3.5–3.6 | 3.1 | 4.3 |
| Width of talonid base, M ₁ | 3.2–3.3 | 2.9 | — |
| Maximum length, M ₂ | 3.6 | 3.6 | 4.7 |
| Width of trigonid base, M ₂ | ?2.9–3.5 | 3.2 | 4.5 |
| Width of talonid base, M ₂ | 3.3 | 3.0 | — |
| Maximum length, M ₃ | 4.3–4.4 | 3.7 | 6.2 |
| Width of trigonid base, M ₃ | 3.0–3.3 | 2.6 | 4.4 |
| Width of talonid base, M ₃ | 2.5–2.6 | 2.1 | — |
| Length of P ₄ –M ₁ | 7.4 | 7.1 | — |
| Length of M ₁ –M ₃ | 11.3–11.4 | ≤11.2 | 14.9 |
| Length of P ₁ –M ₃ | 23.9 | 22.5 ^a | 31.3 |
| Length of P ₂ –M ₃ | 21.1 | 19.5 ^a | 26–27 ^a |

^a Estimated.

dentition; collected at Jhama Obo, “East Mesa,” east of Shara Murun Valley, Inner Mongolia.

STRATIGRAPHIC POSITION: Both specimens are reported to have come from the Ulan Gochu Formation, the type locality of which lies about 14 miles away on the west side of the Shara Murun Valley, on the north side of Baron Sog Mesa. According to Walter Granger’s field notes (MS, p. 19): “It is probable that many of the specimens labelled ‘Shara Murun’ are really ‘Ulan Gochu.’ The line between the two horizons [i.e., Eocene Shara Murun beds below and Ulan Gochu beds above] at Twin Oboes and Jhama Obo was not determined.” Thus either *Anagale* occurs at the base of the correlated Ulan Gochu at this locality (base equals base of upper red beds), or it occurs well up in the correlated Ulan Gochu. The specimens were associated with *Embolotherium* remains.

AGE: Early Oligocene.

DESCRIPTION: P¹ is present and is double-rooted as is that of the type specimen of *Anagale gobiensis* but apparently in contrast to that of *Anagalopsis kansuensis*. The crown is composed of a single cusp with rounded sides, a steep anterior slope, and a less steep posterior cutting edge.

P² is three-rooted, the lingual root supporting a small protoconal swelling like that of the type specimen, but relatively larger than that of *Anagalopsis*, which is not a separate root but merely a lingual extension of the posterolabial root. The protoconal swelling is worn, and I cannot tell whether it once possessed a distinct apex, but it seems likely that it did not. The protoconal swelling is situated posterior to the level of the paracone apex. The latter is high and has a steep anterior slope, but an anterior cutting edge is not present. The posterior cutting edge possesses a slight swelling, which suggests the site of a former metacone. No such structure remains in *Anagalopsis*, and in the type specimen of *Anagale* this area is too worn for observation.

P³ is almost as large as P⁴ and the molars, but differs from them in that the protocone is relatively a much lower and less important cusp. Its apex, like that of P³ of *Anagalopsis*, is essentially a cone tilted forward. The apex of the protocone is opposite the posterior slope of the paracone but is farther forward than on P². The paracone apex is far forward, with a steep but rounded anterior face and a concave posterior cutting edge running to the posterolabial corner of the tooth. A small parastyle was apparently present. The remainder of the labial part of the tooth, like the ectoloph of P⁴ and the molars, has been destroyed by weathering.

P⁴ represents a distinct break from the pattern of more anterior teeth, in that the tooth crown is lingually high and prismatic, as in the type specimen, though not so much so as in *Anagalopsis*. The protocone is massive, high, and has nearly vertical sides. The enamel does not, however, enter the alveolus as it does in *Anagalopsis*. The apex of the protocone is anterolingually placed, and from it a cingulum extends labiad toward the parastyle. A crest curves from the protocone apex posterodorsolabial around the base of the trigon but is not a depressed hypoconal cingulum like that of the molars. It does widen slightly at the position where a hypoconal shelf is present on M¹ and M², but a true hypocone is not present. The labial side of P⁴ has been eroded away, and it is not possible to say whether a metacone was incipiently present behind the paracone. Bohlin (1951) did not report a metacone on P⁴ of *Anagalopsis*, but a very slight swelling is present posterolabial to the paracone on a cast presented to the American Museum of Natural History. A parastyle similar to that of the type specimen can also be seen in the new specimen, in contrast to P⁴ of *Anagalopsis kansuensis*.

M¹ also has its ectoloph eroded away but is sufficiently unworn to demonstrate some of the lingual crown pattern, which is not available or clearly shown in the type specimens of *Anagale gobiensis* or *Anagalopsis kansuensis* because of wear. The steep-sided and linguallly flattened protocone is especially high and prismatic, though its enamel does not extend into the alveolus. A ridge from its worn apex rounds the anterolingual base of the paracone, and another ridge runs to the lingual base of the metacone, but conules are absent, as in *Pseudictops* and possibly also *Eurymylus*. The paracone and metacone are well separated but so damaged that nothing more can be said except that the base of the paracone is more lingual than that of the metacone. Because the tooth is not so worn as that of the type specimen, a worn hypoconal shelf or cingulum, the presence of which was suggested by Simpson, can be clearly seen. The anteroposterior diameter of the trigon is increased dorsal to this point, resulting in the complete abandonment of an interdental embrasure and interlocking occlusion. When the molars wear down to the level of the hypoconal shelf, the occlusal surfaces of all the teeth from P⁴ to M³ merge as a linear series of four oval enamel rings filled with dentine, all oriented in approximately the same plane. The type specimens of both *Anagale gobiensis* and *Anagalopsis kansuensis* have reached that level of wear, and the details of their unworn dental pattern have therefore been erased. The hypoconal shelf appears to terminate posterolingual to the base of the metacone.

M² is somewhat smaller than M¹, but the features are similar. The protocone is high and prismatic, but, like that of M¹, the enamel does not enter the alveolus. The paracone base joins the anterior crest from the protocone, and the latter does not appear to have extended farther labiad. The metacone base is not so linguallly placed as the paracone base. The hypoconal shelf consists of a short cingulum dorsally placed on the posterior trigon wall. The type specimen of *Anagale gobiensis* is worn to that level, and no trace of a hypoconal cingulum remains in *Anagalopsis kansuensis*, either because of wear or evolutionary loss.

M³ is represented only by a narrow protocone, which appears to lack all but a faint trace of a hypoconal shelf. As in the other molars, the enamel does not extend into the alveolus.

P⁴-M³ show the same unilateral, high-crowned condition noted by Bohlin (1951) in *Anagalopsis*, except that in that form the lingual enamel extends into the alveolus. Simpson (1931) did not remark about the lingual high-crowned nature of P⁴-M³ in his original paper, but did note it later in a letter to Bohlin (1951, p. 38). The maxilla extends farther ventrad labial to these teeth than its level on the palate, so that in labial

view there is no clue that the protocone is a high prism. The situation is not unlike what may be seen in tillodonts, and Bohlin has noted a similarity to certain lagomorphs and rodents. There is also a similarity to *Pseudictops*.

P₁–P₃ are poorly preserved on the left lower jaw and missing altogether on the right one. P₁ was double-rooted, but its crown is not preserved. P₂ was probably larger than P₁, double-rooted, and its apex had a steep anterior slope, followed by a more gently inclined posterior slope which



FIG. 1. *Anagale gobiensis*, A.M.N.H. No. 26141, damaged right P¹–M³. The ectolophs of P³–M³ have been eroded away. *Above*: Buccal view, illustrating damage. *Below*: Occlusal view. Both photographs slightly retouched. For associated lower dentition, see figure 2. Both $\times 4$.

met a low heel cusp. Lingual to the heel cusp is a small groove similar to that of P₃. P₃ is larger than P₂ and was double-rooted. The high protoconid apex lies above the anterior root and is preceded by an antero-lingually deflected blade of which the anterolabial surface continues the curve of the labial surface of the protoconid. This blade acts as a paraconid and may have had its own tiny apex about halfway up the anterior wall of the protoconid in very early wear, but the apex is now obliterated, if it ever was present. There is apparently no paraconid blade in *Anagalopsis*, in contrast to *Anagale*. The posterior slope of the protoconid bears two crests, one lingual and extending from the protoconid apex to the anterolingual base of the heel, the other a short crest connecting the middle of the protoconid base with a central heel cusp. The latter is

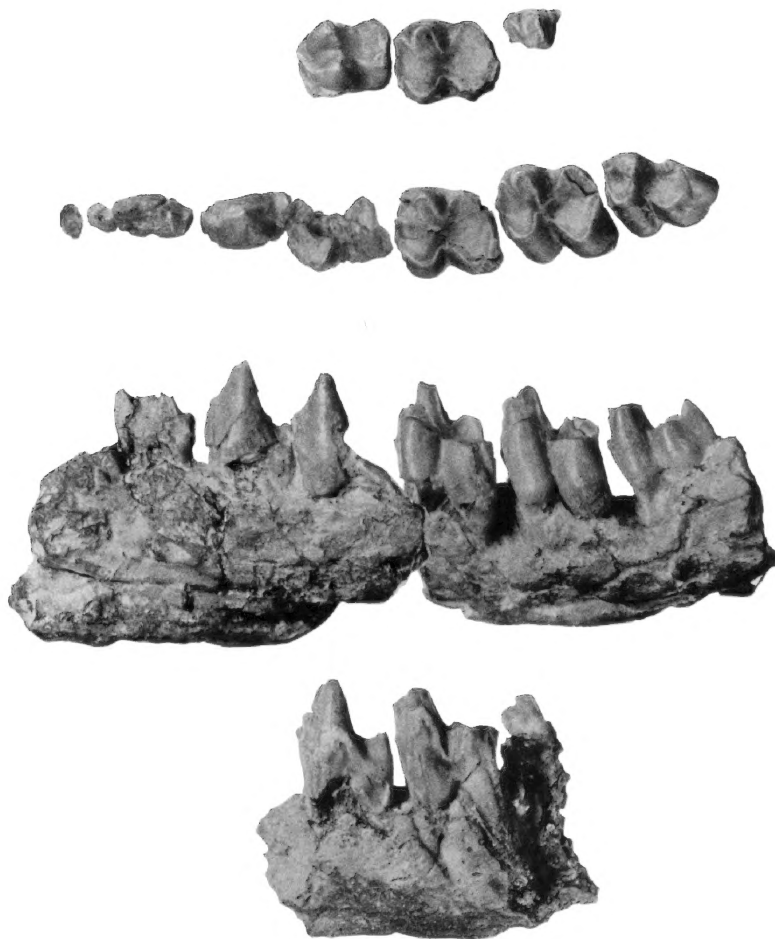


FIG. 2. *Anagale gobiensis*, A.M.N.H. No. 26141, fragmentary but little-worn right and left lower jaws, right lower jaw photographically reversed to facilitate comparison with the right dentition. Homologous teeth aligned. Above: Occlusal views. Below: Buccal views. All photographs slightly retouched, and the left jaw photographically reconstructed from two pieces displaced slightly in the matrix. For the associated upper dentition, see figure 1. All $\times 4$.

flanked lingually by an additional talonid cusp, but there is no true talonid basin.

P_4 offers a sharp contrast to P_3 , though not so sharp a contrast as in *Anagalopsis*. The trigonid consists of two main cusps of about equal height, the protoconid and metaconid. The posterior wall of the trigonid

is flat and M-shaped, the lingual border of the metaconid straight, and the labial border of the protoconid convex. A low paralophid descends from the anterior crest of the protoconid, curving linguad to terminate at the anterior base of the metaconid. Two low swellings on this crest take the place of a paraconid. Bohlin thought that there might be a reduced paraconid on P_4 of *Anagalopsis kansuensis*, but I am unable to see it on a cast or in Bohlin's figures. A short anterior cingulum rises from the antero-lingual base of the protoconid toward the lingual end of the paralophid but terminates before reaching that point. A broad basined heel is present, rimmed by a metastylid, entoconid, hypoconulid, hypoconid, and crista obliqua. The metastylid is a tiny cuspule at the posterolingual base of the metaconid. Posterior to the metastylid is a deep lingual notch, followed by a small conical entoconid. The basin rim turns at this point and is continued by a transversely elongate hypoconulid which may have had more than one apex. The hypoconulid is situated lingual to the mid-line of the tooth. The hypoconid comprises the posterolabial corner of the talonid, and its posterior wall is in line with the hypoconulid, so that the transverse talonid crest noted by Simpson (1931) in the type specimen consists of the usual three posterior talonid cusps. A similar posterior talonid crest occurs in *Pseudictops*. The anterior crest of the hypoconid (crista obliqua) is not oblique but runs straight forward to join the posterior trigonid wall at the middle of the base of the protoconid. The labial wall of the hypoconid and crista obliqua slopes labiad toward the base of the crown in order to occlude with the large P^4 paracone.

M_1 , like M_2 and M_3 , has the trigonid sufficiently unworn to demonstrate the pattern. In the type specimens of *Anagale gobiensis* and *Anagalopsis kansuensis* the cheek-teeth trigonids are worn down almost to the level of the talonids. The trigonid is formed primarily by the metaconid and protoconid, but anterior to the metaconid lies a closely appressed paraconid which juts forward from the metaconid, well above the level of the talonid floor. Below the base of the paraconid is a brief horizontal anterior cingulum in contact with the hypoconulid of P_4 . The heel is short and diamond-shaped, with a continuous rim of enamel raised at the locations of the hypoconid and entoconid. The shape is reminiscent of the talonids of *Eurymylus*, but the enamel does not thin on the anterior sides of the hypoconid and entoconid. The pattern of M_1 is not fundamentally distinct from that of M_1 of *Pseudictops*, though the talonid is narrower in that form.

M_2 is slightly larger than M_1 . On M_2 of the type specimen the trigonids of both the right and left teeth possess a labial styler cusp arising from the side of the protoconid base. Above this cusp the trigonids of the type

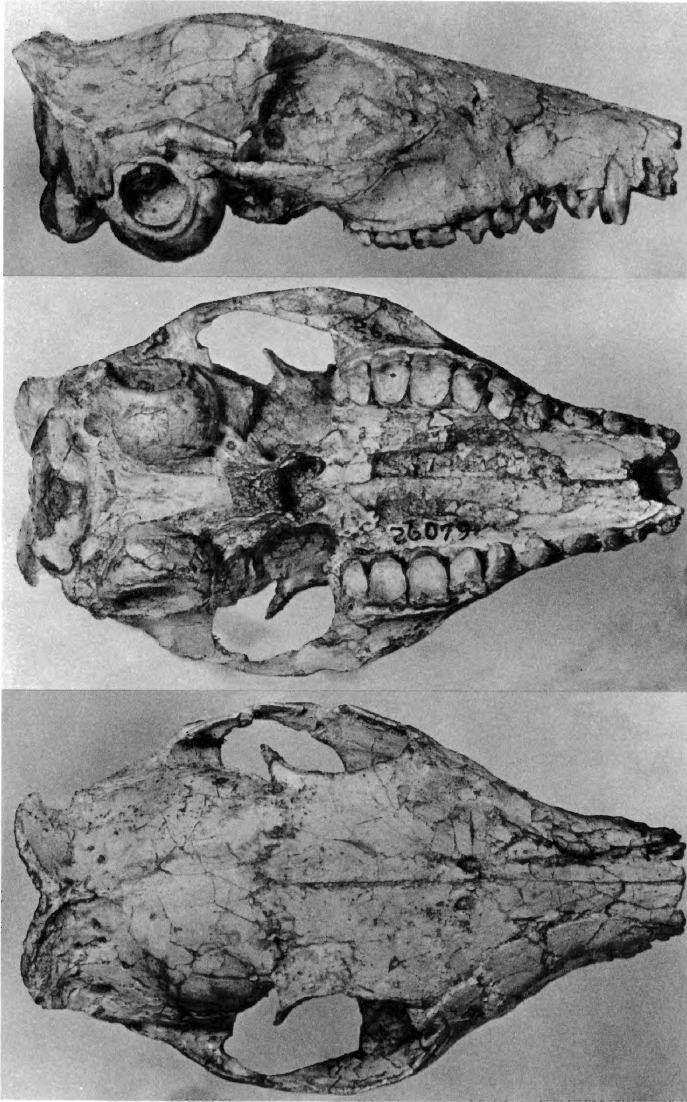


FIG. 3. *Anagale gobiensis*, type specimen, A.M.N.H. No. 26079. *Top*: Lateral view. *Center*: Ventral view. *Bottom*: Dorsal view. All $\times 1.5$.

specimen narrow, which may indicate individual variation. Otherwise M_2 has the same pattern as M_1 in both specimens. The wide talonid of M_2 diverges from that of *Pseudictops*.

M_3 possesses a distinct paraconid and a short anterior cingulum, which

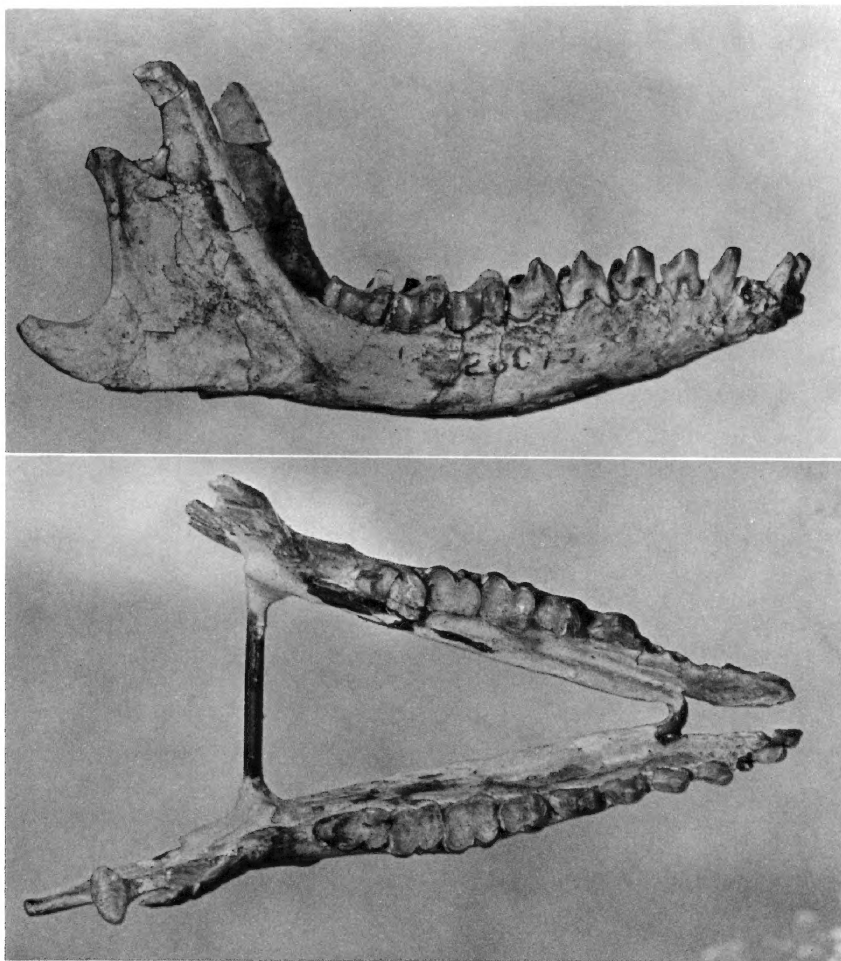


FIG. 4. *Anagale gobiensis*, type specimen, A.M.N.H. No. 26079. *Above*: Lower jaws in lateral view, left ramus deëmphasized and left dentition not shown. *Below*: Occlusal view. Both $\times 2$.

cannot be seen on the other anagalid third lower molars because of wear. The hypoconid is large, the entoconid small, and the hypoconulid large and projecting to the rear.

P_4-M_3 show a feature also seen in tillodonts, in that the labial enamel of the teeth extends farther down the roots than does the lingual enamel. This feature is correlated with the unilateral, lingual, high-crowned nature of P^4-M^3 .

Extensive comment on the non-tupaoid nature of the anagalid denti-

tion probably would not be fruitful at this time. As can be seen at a glance, there is little special similarity to the dentition of any living tupaoid. The tupaoids and anagalids certainly had a common ancestor, as did all mammals at some point, but the question is really whether anagalids and tupaoids had a common ancestor that was itself in a lineage distinct from other mammalian groups. Demonstration of special affinity between the anagalids and tupaoids would require, among other things, distinctive dental characters held in common that could not be derived with equal or greater probability from the dentitions of an assortment of known early Cenozoic families arrayed in a number of mammalian orders, and such a demonstration is not possible at present. Even in orders in which a truly primitive dentition is not yet known, such as the Lagomorpha, it may be expected that a generalized, potentially "pre-anagalid" dentition will be found to exist in the earliest, presently unknown members of the order. By Oligocene time anagalids had become sufficiently distinct from all other known mammals, so that on the basis of the dentition one cannot determine at present which of several potentially ancestral groups was actually ancestral to the Anagalidae. The dentition of anagalids, therefore, does not solve the vexatious problem of anagalid affinities. What is now required is the finding (or recognition) of pre-Oligocene anagalids.

THE ANAGALID AUDITORY BULLA

Simpson (1931) believed that the bulla of *Anagale* was probably composed wholly of an entotympanic ossification and that the tympanic ring was situated within the bulla. An exposure of bone within the damaged left bulla was identified as a fragment of the tympanic ring, but preparation techniques were not sufficiently advanced at that time to permit further investigation. Bohlin (1951) suggested that what Simpson had identified as part of the tympanic ring may have been a fragment of one of the auditory ossicles. If it could be accepted that the bulla of *Anagale* is wholly entotympanic in origin, then that evidence would weigh heavily in favor of prosimian or leptictid affinities for the anagalids, but unfortunately it cannot be accepted, as has already been suggested for *Anagalopsis* by Bohlin.

The bone identified as a fragment of the tympanic ring by Simpson has now been prepared by means of an Airbrasive machine and proves to be merely part of the bullar wall. It is not even a projecting part of the wall. A bit of matrix lying in a depression in the broken edge of the wall led to the impression that two bones were involved, whereas only one is present. Thus there is no evidence of either a separate tympanic ring within the

bullae or the remains of an auditory ossicle. Simpson was right, however, in his identification of the structure as part of the tympanic, because the bulla of *Anagale* is almost unquestionably a compound ossification composed of both a tympanic and an entotympanic bone. Symmetrically exposed on both right and left bullae are what appear to be ankylosed sutures between the entotympanic and tympanic parts of the bulla. If this interpretation is correct, the entotympanic would be a structure lying against the petrosal, basisphenoid, and alisphenoid, but not fused to



FIG. 5. *Anagale gobiensis*, type specimen, A.M.N.H. No. 26079. Oblique view of right ear region of skull. $\times 3$.

them. The anterior end of the entotympanic of *Anagale* lies dorsomedial to the medial pterygoid lamina. Posterior to this point the entotympanic possesses a descending wing, the medial wall of the bulla. About 2 mm. ventral to the level of the fused basioccipital-basisphenoid bones, the distal edge of the entotympanic meets the tympanic, which continues as the bullar floor. Bohlin saw no such suture in the type specimen of *Anagalopsis kansuensis*, but that specimen is also an old individual in which the ankylosis may be difficult or impossible to see.

Careful removal of the matrix filling the left bulla of the skull of *Anagale gobiensis* has revealed a thin bony septum the ventral surface of which is continuous with the bullar floor. The septum is attached to the bulla opposite the location of the suspected ankylosed suture visible on the outer surface of the bulla. Its dorsomedial base may incorporate bone of

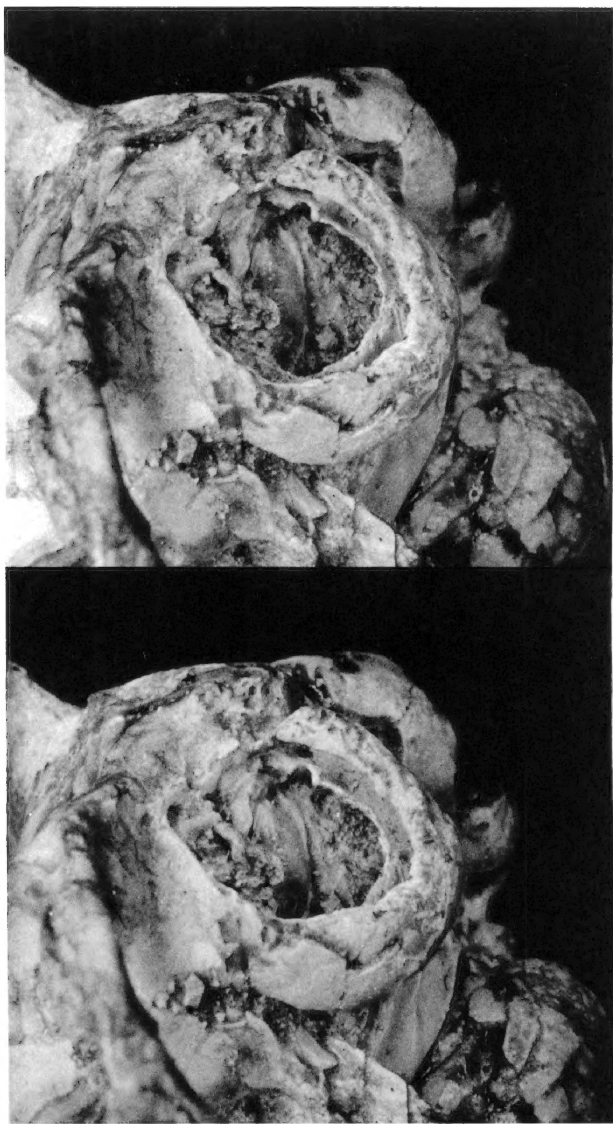


FIG. 6. Oblique stereoscopic photograph of the left bulla of *A.M.N.H.* No. 26079, type of *Anagale gobienus*. Matrix within the bulla has been removed, uncovering for the first time the septum bullae and the bony attachment of the tympanic membrane. These features and others demonstrate the tympanic nature of most of the bulla. The entotympanic component of the left bulla is not visible from this angle. Approximately $\times 3.6$.

entotympanic origin, but the ventral face of the septum and all of the bulla ventrolateral to that point are viewed here as part of an expanded tympanic ring. The tympanic membrane appears to have been vertical and attached to the tympanic bulla just medial to the external auditory meatus. Fragments of the malleus may be present near the promontorium of the petrosal bone, but these are newly exposed and are not the structures discussed by either Simpson or Bohlin.

Thus, *Anagalopsis* and *Anagale* agree with each other in the major features of bullar construction, and anagalids are not so similar to tupaioids (Saban, 1956–1957) in bullar morphology as past interpretations would have them be.

ANAGALID FEET

The remarkable feet of *Anagale* were described by Simpson but were only briefly discussed. The peculiar combination of large fissured claws of the manus and distally spatulate unguals of the pes is very uncommon in mammals, and, in fact, I know of only one other family of mammals, living or extinct, in which this condition is approached: the Didymoconidae Kretzoi, 1943 (=Tshelkariidae Gromova, 1960). Even in the Didymoconidae the posterior unguals are not fissured, whereas they are fissured in *Anagale*.¹ Gromova's description of the feet of *Tshelkaria* is striking. The resemblance between the two genera extends to the astragalus as well, though an astragalar foramen is lacking (Gromova, 1960, p. 55) in *Tshelkaria*.²

The fissured condition of the unguals is unlike the condition seen in tupaiid feet, in which the claws are narrow and unfissured, as in Recent Insectivora. The fissured condition is apparently primitive and is characteristic of some very ancient groups, such as didymoconids, mesonychids, pangolins, lagomorphs, hyaenodonts, oxyaenids, hyopsodonts, and even *Plesiadapis*, but similarities to these are not detailed enough to allow any conclusions other than that in this feature *Anagale* resembles them more than it resembles the Tupaiidae and other lemuroids advanced beyond plesiadapids. The broadening of the rear unguals does resemble the condition seen in various advanced prosimians, including lemurs as noted by Simpson, but lemur unguals are not fissured.

¹ The illustration given by Piveteau (1957, p. 35, fig. 24) of the pes of *Anagale*, derived from Simpson's accurate illustration, does not depict the ungual fissures.

² Another resemblance between didymoconids and anagalids consists of the short premaxillary bones in both families.

THE GEOLOGIC AGE OF *ANAGALOPSIS*

A major problem in the interpretation of *Anagalopsis* is that its age has not been determined with any degree of certainty. Bohlin was cautious about the matter, stating (1951, p. 9) that the age of the locality is unknown, but probably somewhere in the earlier half of the Tertiary (p. 7). In his discussion of the affinities of *Anagalopsis*, Bohlin stated that "... there are reasons to suspect that *Anagalopsis* is the descendant from some form identical with or closely related to *Anagale*, but that as long as the question about the bulla is not settled—and it may be settled either way—no definite conclusion can be drawn." Now that the question is settled, it would seem probable that *Anagalopsis* is from a deposit younger than the Ulan Gochu Formation, which is believed to be of Early Oligocene age. Patterson (1954, p. 198) reached the same conclusion, suggesting that the age of *Anagalopsis* may fall somewhere in the later Oligocene, but Wood (1959, p. 354) has suggested that the age may be Paleocene on the basis of *Mimolagus*, a primitive *Eurymylus*-like lagomorph (but with P²) from the same locality. Central Asia is almost unquestionably the ancestral home of the Lagomorpha, however, and to find Oligocene survivors of an earlier lagomorph radiation would not be surprising. Actually, still another mammal occurs at the same locality, and there are some undescribed fossil turtles. The mammal was tentatively identified by Bohlin (p. 46) as an ungulate and possibly an artiodactyl about the size of a small pig. The age of all these remains is therefore regarded here as ?Oligocene.

CONCLUSIONS

New evidence of the dentition of *Anagale* and a reconsideration of several aspects of known anagalid osteology, the ear region and the feet, remove several crucial reasons for considering the Anagalidae to be specifically related to the Tupaioidea, but do not shed much light on the true affinities of the anagalids. That they are primitive eutherian mammals is not in question, but their known occurrence in the mid-Tertiary surely indicates a long period of isolation in temperate Central Asia, when they and their close taxonomic allies evolved at a variety of rates and in a sufficient number of ways to make identification of the closest anagalid relatives hazardous. The anagalids are not primates but seem to represent an Oligocene hold-over of some early Cenozoic or even late Mesozoic stock which became adapted to digging with its powerful front feet. The suggestion is not made that *Anagale* and *Anagalopsis* were fossorial, but the diet may have been obtained from below the surface of the ground, as is

also suggested by the extreme wear of the teeth and the anagalid response to that condition: a trend toward dental hypsodonty. Therefore the argument of Bohlin (1951) is endorsed, and the Anagalidae are referred to the Eutheria, *incertae sedis*.

REFERENCES

BOHLIN, B.

1951. Some mammalian remains from Shih-ehr-ma-ch'eng, Hui-hui-p'u area, western Kansu. In Hedin, Sven, Reports from the scientific expedition to the north-western provinces of China. Stockholm, vol. 6, Vertebrate paleontology 5, pp. 1-47, figs. 1-83, pls. 1-7.

GRANGER, W.

- [MS.] Mongolia. 1928. Central Asiatic Exped[ition] record of fossils. New York, the American Museum of Natural History, field book in the Osborn Library.

GROMOVA, V.

1960. O novom semeistve (Tshelkariidae) primitivnikh khishchinkov (Creodonta) iz oligotsena Azii. Trudy Paleont. Inst., Akad. Nauk, U.S.S.R., vol. 77, pp. 41-78, 16 figs., 4 pls., paged.

KRETZOI, M.

1943. *Kochictis centennii* n. g. n. sp., az egeresi felső Oligocénből. Földtani Közlöny, vol. 73, pp. 10-17, pl. 1 (German translation, *ibid.*, vol. 73, pp. 19-195, 283).

PATTERSON, B.

1954. The geologic history of non-hominid primates in the Old World. Human Biol., vol. 26, no. 3, pp. 191-209, figs. 1-3.

PIVETEAU, J.

1957. Primates, paléontologie humaine. In Piveteau, J., Traité de paléontologie. Paris, Masson, vol. 7, 675 pp., 639 figs., 8 pls.

SABAN, R.

- 1956-1957. Les affinités du genre *Tupaia* Raffles 1821, d'après les caractères morphologiques de la tête osseuse. Ann. Paléont., vol. 42, pp. 169-224, figs. 1-26; vol. 43, pp. 1-44, figs. 27-41, pls. 1-3.

SIMPSON, G. G.

1931. A new insectivore from the Oligocene, Ulan Gochu horizon, of Mongolia. Amer. Mus. Novitates, no. 505, pp. 1-22, figs. 1-5.

WOOD, A. E.

1959. Eocene radiation and phylogeny of rodents. Evolution, vol. 13, no. 3, pp. 354-361, 2 figs.